A NEW GENUS OF MARSUPIATE SPATANGOID ECHINOID FROM THE MIOCENE OF SOUTH AUSTRALIA

K. J. MCNAMARA & D. J. BARRIE

MCNAMARA, K. J. & BARRIE, D. J., 1992. A new genus of marsupiate spatangoid echinoid from the Miocene of South Australia. *Rec. S. Aust. Mus.* **26**(2): 139–147.

The southern Australian Tertiary fossil record contains a relatively rich fauna of marsupiate echinoids. The 10 species currently known are placed in five genera, and are supplemented by this description of a new genus and species of marsupiate spatangoid echinoid, *Hysteraster paragrapsimus* gen. et sp. nov. Collected from the late Early Miocene to early Middle Miocene Morgan Limestone on the banks of the Murray River, South Australia, this new form is characterised by the possession in the female of deeply sunken apical system and petals on the aboral surface. The male of this genus can be distinguished from the female by its much smaller gonopores and lack of sunken petals. The genus is placed in the family Brissidae and, as such, is the first record of a marsupiate genus in this family.

K. J. McNamara, Department of Earth and Planetary Sciences, Western Australian Museum, Francis Street, Perth, Western Australia 6000, and D. J. Barrie, PO.Box 227, Coonalpyn, South Australia 5265.
Manuscript received 7 April 1992.

The Tertiary rocks of southern Australia contain one of the richest echinoid faunas of this age in the world, with some 60 genera having been described (McNamara in prep.). A characteristic feature of this fauna is the presence of marsupiate echinoids - those echinoids that bear depressions in their test that were used for brooding the young. To date some 10 marsupiate species have been described from the Tertiary rocks of southern Australia, all by Philip & Foster (1971). At the time of their publication only one other Tertiary marsupiate echinoid was known from elsewhere in the world: *Abatus pseudoviviparus* (Lambert), from the Paleocene of Madagascar. However, since then Roman (1983) has described a further four species from the Middle Miocene and Pliocene of western Europe. Of this total of 15 Tertiary species, only three are spatangoids: *Abatus pseudoviviparus*, and the two species of *Peraspatangus* that Philip & Foster (1971) described from Australia, *P. brevis*, from the Early Miocene, and *P. depressus* from the Middle Miocene.

The discovery of two specimens by one of us (J. B.) of a hitherto undescribed spatangoid genus from the late Early to early Middle Miocene Morgan Limestone downstream of Waikerie on the banks of the Murray River, therefore brings to three the number of marsupiate genera of spatangoid echinoids now known from the Tertiary. A single specimen in the collections of the Museum of Victoria is also referred to this genus, as is a specimen from Wigley Reach, near Overland Corner on the Murray River in the collections of the South Australian Museum. Although lacking the sunken petals and apical system characteristic of the females, the other test characters appear to be sufficiently similar to indicate that this lone specimen is the male of the species.

Stratigraphy

The Morgan Limestone, from which the type specimens were collected, outcrops along the bank of the Murray River in the vicinity of Morgan. In its type section, six kilometres south of Morgan, the unit reaches a thickness of about 30 m (Ludbrook 1961). In some parts of the Murray Basin it is up to 100 m thick (Ludbrook 1969). The Morgan Limestone straddles the Early to Middle Miocene boundary in age (Australian stages Batesfordian to Balcombian, Lindsay 1985). The dominant echinoid is a clypeasteroid, *Monostychia* sp. Other echinoids collected from this unit include *Phyllacanthus clarkii* (Chapman & Cudmore) (Philip 1963); *Goniocidaris murrayensis* Chapman & Cudmore (Philip 1964); *G.? pentaspinosa* Chapman & Cudmore (Philip 1964); *Delocidaris prunispinosa* (Chapman & Cudmore) (Philip 1964); *Menocidaris compta* Philip 1964; *Murravechinus paucituberculatus* (Gregory) (Philip 1965); *Cryptechinus humilior* (Bittner) (Philip 1969); *Ortholophus morganensis* Philip 1969; *O. pulchellus* (Bittner) (Philip 1969); *Schizaster (Schizaster) abductus* Tate (McNamara & Philip 1980); *Pericosmus compressus* (Duncan) (McNamara & Philip 1984); *Protenaster antiaustralis* (Tate) (McNamara 1985); *Cyclaster archeri* (Tenison Woods) (McNamara *et al.* 1986); *Eupatagus rotundus* Duncan (Kruse & Philip 1985); and *E. ludbrookae* Kruse & Philip 1985.

Material and Methods

The material described in this paper is deposited in the collections of the South Australian Musuem (SAM) and the Museum of Victoria (MV). Measurements were carried out using electronic callipers to a precision of ±0.1 mm. Relative sizes of features of the test are expressed as percentages of maximum test length (%TL).

Systematic Palaeontology

Order Spatangoida Claus, 1876

Family BRISSIDAE Gray, 1855

Genus *Hysteraster* gen. nov.

Etymology

From the Greek *hystera*, meaning 'womb', and *aster*, meaning "star", alluding to the formation of the marsupium from the star-shaped petals.

Diagnosis

Test moderately large, relatively narrow and with slight anterior notch. Apical system set well anterior of centre; deeply depressed in females. Petals short, broad and deeply depressed in females, only slightly depressed in males; do not extend to peripetalous fasciole; pore pairs very reduced in size in anterior rows of anterior petals; in all petals pore pairs absent in vicinity of apical system. Apical system ethmolytic with four gonopores. Peripetalous and subanal fascioles present. Aboral tubercles much larger within peripetalous fasciole than outside of it; those in interambulacra 2b and 3a are the largest and most sparsely distributed. Peristome subcentral. Plastron small, with prominent posterior keel. Periplastronal area wide.

Remarks

There seems little doubt that the deeply sunken petals in *Hysteraster*, combined with a deeply sunken apical system, functioned as a marsupium. This is supported by the presence of large gonopores in the female (see below). *Hysteraster* ean be distinguished from all other marsupiate spatangoids by its possession in the female of both deeply sunken apical system and deeply sunken petals. In the living spatangoids *Abatus* and *Tripylus*, which also have deeply sunken petals, the apical system is not depressed at all. The only spatangoid to share the combination of sunken aboral ambulacra and apical system is the Australian Tertiary genus *Peraspatangus*. However, in this genus just a simple depression is formed, comprising the apical system, the adapical ambulacra and interambulacra, whereas in *Hysteraster* the adapical interambulacra are not sunken. Unlike *Peraspatangus*, with its non-petaloid adapical ambulacra, pore pairs are present in the marsupium in *Hysteraster*, although they do degenerate in the vicinity of the apical system and in the anterior rows of the anterior petals.

One of the specimens, SAM P24260 (Fig. 2) shows the presence of a well developed subanal fasciole. Consequently it is possible to place *Hysteraster* within the Brissidae with confidence as a peripetalous fasciole is also present. Furthermore, the overall appearence of the test, the presence of a prominent plastronal keel, a feature usually present in those genera possessing a subanal fasciole, and the development of larger tubercles within the peripetalous fasciole, support the emplacement of *Hysteraster* within the Brissidae. This is the first record of a marsupiate genus within this family. Although a few other brissid genera, such as *Rhynobrissus*, *Macropneustes*, *Meoma* and *Schizobrissus* have sunken petals, they are much shallower than in *Hysteraster*, and there is no evidence that such forms were marsupiate.

The male *Hysteraster* can be distinguished from other brissids by the nature of its relatively short, broad, slightly sunken petals; its very anteriorly situated apical system; degenerate pore pairs in the anterior row of the anterior petals and distinctive aboral tuberculation. The only other genera that possess some of these characters are *Migliorina* and *Plesiopatagus*. However, *Hysteraster* differs from the former in possessing larger tubercles inside the peripetalous fasciole, and from the latter in its possession of four, rather than two, gonopores. Furthermore, neither of these two genera is known to be marsupiate.

One of the characteristic features of *Hysteraster* is the failure of the anterior paired petals to reach the peripetalous fasciole (Fig. 4). There are few other spatangoids which share this attribute, but one is the living marsupiate *Tripylus*. However, in the other living marsupiate spatangoid, *Abatus*, the anterior petals do reach the fasciole. An unusual feature of *Hysteraster* is the presence of the enlarged primary tubercles, not only on the interambulacra within the peripetalous fasciole, but also in ambulacra II and IV between the ends of the petals and the fasciole. Selective pressure for the presence of primary tubercles must have been particularly strong.

Hysteraster paragrapsimus sp. nov.

(Figs 1–4)

Etymology

From the Greek '*paragrapsimos*', meaning 'exceptional', in reference to the extent of development of the marsupium.

Material

Holotype: SAM P32322, from the late Early to early Middle Miocene Morgan Limestone, Murray River cliffs, downstream from Waikerie at Broken Cliffs, South Australia.

Paratypes: SAM P32323 from the same horizon and locality as the holotype; SAM P24260, probably

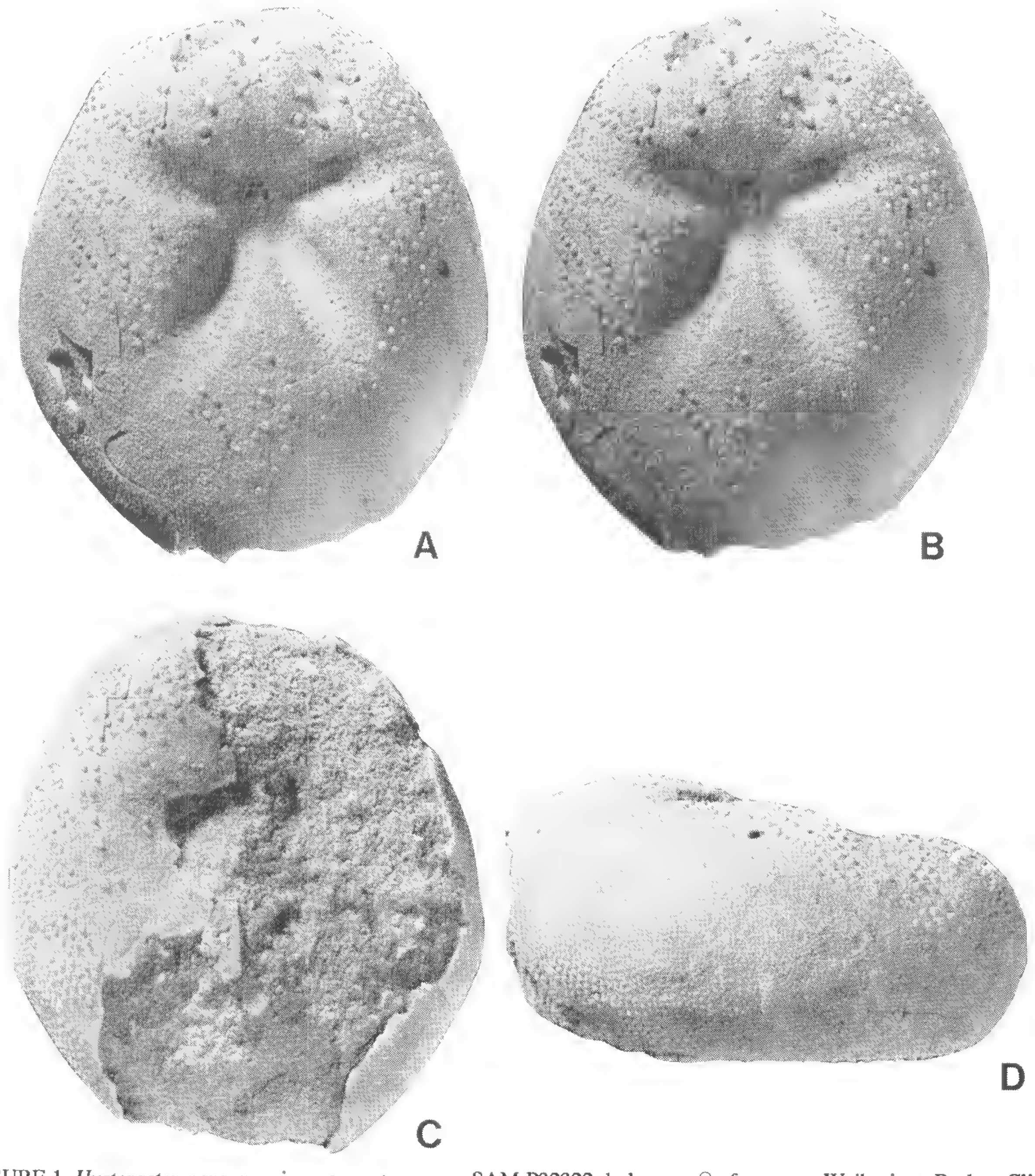

FIGURE 1. *Hysteraster paragrapsimus* gen. et sp. nov. SAM P32322, holotype, ♀, from near Waikerie at Broken Cliffs, Murray River, South Australia; Morgan Limestone; A and B stereopair of aboral surface; C, adoral surface; D, lateral view; all x1.3.

from the same horizon at Wigley Reach, near Overland Corner, Murray River cliffs; and MV 18039, probably from the Morgan Limestone near Morgan, South Australia. Mr F. Holmes (pers. comm.) informs us that no locality details are entered for this specimen in the catalogues of the Museum of Victoria. However, it is registered with a suite of specimens that was collected by F. A. Cudmore form the Morgan Limestone in the vicinity of Morgan.

Diagnosis

As for the genus.

Description

Test moderately large, reaching up to 54 mm TL in females; male has test length of 30.5 mm; ovate, with a very faint, broad anterior notch in some specimens and broadly rounded ambitus; highest posteriorly in interambulacrum 5, midway between apical system and posterior ambitus; height 50–55%TL in females, 55%TL in male; test longer than wide, width ranging between 84–88%TL in females and 83%TL in male; widest posterior of centre. Aboral surface plunges steeply anteriorly (Figs 1D, 2E). Apical system anteriorly eccentric, 27–30%TL from anterior

FIGURE 2. *Hysteraster paragrapsimus* gen. et sp. nov. SAM P24260, paratype, ♀, from Wigley Reach, near Overland Corner, Murray River, South Australia; Morgan Formation; A and B, stereopair of aboral surface; C, posterior view; D, adoral surface; E, lateral view; all x1.3.

ambitus in females, 32%TL in male and extremely deeply sunken in marsupium in females, up to 56%TH from apex of test in paratype female; only slightly sunken in male; ethmolytic, with four gonopores; very large in females (Fig. 1A,B); very small in male, one-seventh the female width; anterior pair in female circular, in holotype 1.3%TL in diameter; posterior pair pear-shaped, long axis 2%TL; madreporite extends slightly beyond posterior gonopores (Fig. 4).

Ambulacrum III narrow and not sunken close to apical system, becomes a little wider and very slightly sunken as crosses anterior ambitus; pore pairs extremely small; number not known. Petals relatively short, broad, although narrowing distally, and open distally; distal one-third not sunken; proximal two-thirds deeply sunken in females, plunging to deeply sunken apical system (Figs 1A,B; 2A,B; 3A,B; 5); slightly sunken in male (Fig. 3G). Anterior petals straight, broad, width 8–9%TL; diverge anteriorly at about 150°; short, 18–19%TL; bear up to 12 pore pairs within petals, those in ambulacra IIb and IVa very reduced in size (Fig. 4), about one-third size of those in IIa and IVb; pore pairs degenerate at about one-quarter petal length from apical system in poste-

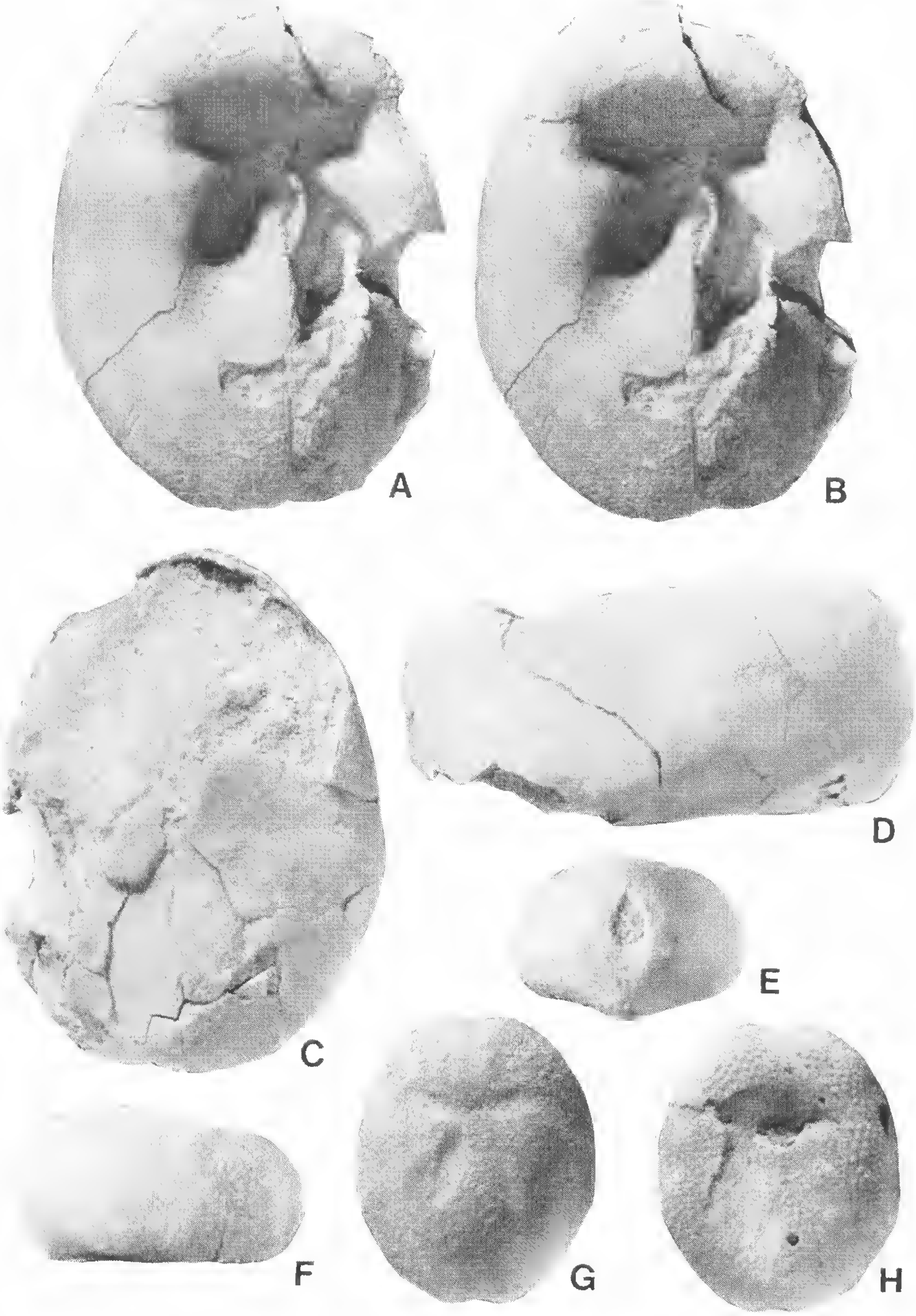

FIGURE 3. *Hysteraster paragrapsimus* gen. et sp. nov. **A-D**, SAM P32323, paratype, ♀, from near Waikerie at Broken Cliffs, Murray River, South Australia; Morgan Limestone; A and B, stereopair of aboral surface; C, adoral surface; D, lateral view. **E-H**, MV P18039, paratype, ♂, probably from the Morgan Limestone near Morgan, South Australia; E, posterior view; F, lateral view; G, aboral surface; H, adoral surface; all x1.3.

rior row; pores slightly elongate proximally, becoming circular distally, not conjugate. Posterior petals longer than anterior, being 31–35%TL; bear up to 17 pore pairs; pores in each poriferous tract of similar size; reduced adapically; slightly broader than anterior petals, being 10–11%TL; petals diverge posteriorly at about 50°.

Peripetalous fasciole quite narrow, about 1.5%TL in width; not indented between anterior and posterior petals; runs along the ambitus anteriorly, and close to the ambitus opposite anterior petals; both anterior and posterior petals fail to reach the fasciole (Fig. 4). Subanal fasciole subtends a chevron shape outline (Fig. 2C) that is 35%TL in width; fasciole twice width of peripetalous fasciole.

Aboral tubercles very variable in size; outside of the peripetalous fasciole towards the ambitus very densely distributed and small, up to a diameter of 0.3 mm; within the peripetalous fasciole in interambulacra 1, 4, 2a, 3b and 5 tubercles larger and more sparsely distributed, up to a diameter of 0.9 mm; these are also present in ambulacra II and IV between ends of petals and peripetalous fasciole; in interambulacra 2b and 3a they are larger still adapically (Fig. 1A,B) and even more sparsely distributed, with up to eight crenulate tubercles that reach 1.25 mm in diameter.

Adoral surface gently convex. Peristome slightly sunken; width 15–18%TL; anterior situated 28–32%TL from anterior ambitus (Fig. 2D). Phyllode comprises 6 small unipores in ambulacra I, II, IV and V; 3 in ambulacrum III. Labrum short, 5%TL; not projecting anteriorly across peristome. Plastron narrow, length 40%TL; width 25–28%TL; almost flat, but forming a prominent keel posteriorly (Fig. 3E). Periplastronal area wide (Figs 1C; 2D; 3C,H), up to 17%TL. Periproct oval, long axis vertical (Fig. 3E), 15%TL. Adoral tuberculation relatively sparse, but becoming more dense adambitally; tubercles up to 0.8 mm in diameter.

Discussion

Most of the slight differences that are observed between the three female specimens and the sole male probably relate to the size difference between the females and the male, the latter being only slightly more than half the size of the former. These differences include relative test height, test width and position of the apical system. Whether or not the size difference itself is a sexually dimorphic feature is not clear. While a greater range of specimens would be required before this could be ascertained, Kier (1969) and Smith (1984) have noted that female echinoids are often larger than males.

In addition to the obvious reflection of the sexual dimorphism, namely the presence of the marsupium of the female and its absence in the male, the difference in gonopore size between the females and the male is another sexually dimorphic feature. Such dimorphism has been documented in some echinoid species by a number of authors, *e.g.*, in *Pentedium* by Kier (1967), in *Echinocyamus* and *Oligopygus* by Kier (1969), in *Echinocardium* by David *et al.* (1988) and in *Hemiaster* by Jagt & Michels (1990); see also Emlet (1989). However, whereas the difference in gonopore diameter in these non-marsupiate forms never differs by more than a factor of two, in *Hysteraster*, and in the other Australian Tertiary marsupiate spatangoid *Peraspatangus*, it is much greater, presumably to accomodate the larger eggs produced by these brooding species.

Wray & Raff (1991) have noted how echinoids that produce the largest eggs are brooding species, egg size ranging between 1 and 2 mm in diameter. Emlet (1989) has observed that marsupiate echinoids in general have particularly large gonopores, relative to their body size, presumably to accommodate the large eggs. The gonopores of female *H. paragrapsimus* reach up to 1.2 mm in diameter. In *Peraspatangus brevis* Philip & Foster, 1971 the female gonopores are nearly four times the diameter of the male gonopores (Philip & Foster 1971, pl.133, fig. 4). In *Hysteraster paragrapsimus* it is even greater, the gonopores in the larger female (Fig. 1A,B) being about seven times the diameter of those of the male. However, this is in part a function of the differences in test size between the male and female forms. Emlet (1989) has noted that there is a positive relationship between increasing test size and increasing gonopore size. For instance he has shown how in males of the living marsupiate echinoid *Amphineustes lorioli* there is an approximate doubling in size of the gonopores as the test length doubles. In females the allometric coefficient is even greater (see Emlet 1989, figure 3). In *Hysteraster paragrapsimus* the extent of increase in females is likely to be as great.

Although *Hysteraster paragrapsimus* and the two species of *Peraspatangus* are the only spatangoids that possess a marsupium that is constructed from a combination of sunken petals *and* apical system, there is one feature in which the two genera differ from one another. In *Peraspatangus* the ambulacra in the marsupium do not possess any pore pairs. While they are present in the marsupium in *Hysteraster* they are very much reduced in the vicinity of the apical system and in the anterior rows of the anterior petals (see Fig. 4).

There is some difference in the degree of development of the marsupium in the female specimens of *Hysteraster paragrapsimus*. In the paratype SAM P32323 the marsupium attains a depth that is nearly twice that of the marsupium of the holotype. However, as the two specimens are virtually identical in all other respects, it is considered that this difference merely reflects intraspecific variation. The smaller female specimen (SAM P24260) has a marsupium

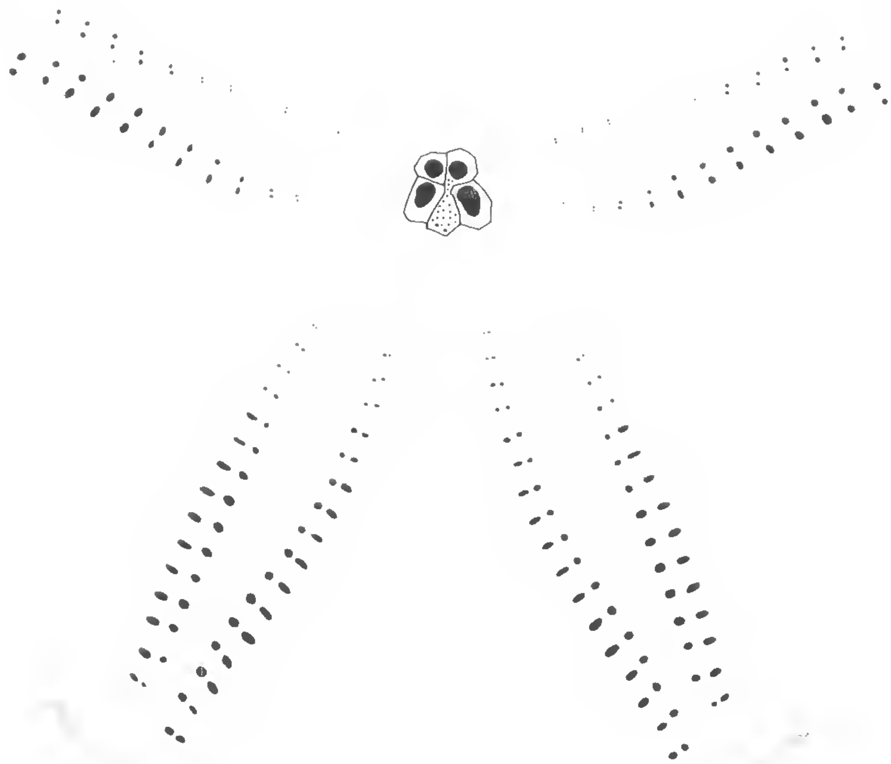

FIGURE 4. Drawing of pore pairs in petals of *Hysteraster paragrapsimus* gen. et sp. nov., holotype, ♀, SAM P32322. Note reduction in size of pore pairs adapically; large gonopores; and failure of pore pairs to reach the peripetalous fasciole.

that is similar in depth to that of the holotype, but the adapical interambulacra surrounding the marsupium are more swollen in this smaller specimen, so enhancing the effective depth of the marsupium.

Functional morphology of *Hysteraster*

Certain characteristics of the test indicate that *Hysteraster* shares the distinction, along with the living spatangoids *Abatus* and *Tripylus*, of being the only echinoderms known to brood their young while buried in the sediment. The existence of a well developed peripetalous fasciole, combined with the wedged shape profile of the test indicate that *Hysteraster* lived completely buried in the sediment. Peripetalous fascioles are a prerequisite for spatangoids that completely burrow in the sediment, while McKinney (1988) has observed that a wedged shape test is often found in spatangoids that burrow in relatively fine-grained sediments, such as those in which *Hysteraster* are preserved. Other brissids that, like *Hysteraster*, possess larger primary spines on the aboral surface are interpreted as being shallow burrowers, with their aboral surface just covered by sediment (McNamara 1991). Further evidence that these genera brooded their young while buried in the sediment is afforded by the preservation of tiny juveniles in the petals of two specimens of the Paleocene species *Abatus pseudoviviparus* (see Lambert 1933, pl. 4, figs 5–7). Such preservation could only occur if there was no disturbance to the specimen after its death, such as would have been the situation with a specimen completely buried by sediment – it was 'preadapted' to being fossilised.

In the case of these burrowing marsupiate spatangoids, following their 'birth' the young echinoids would have nestled in the deep marsupium on the aboral surface of the test (Fig. 5). This method of brooding could have provided the young with exceptional protection from predators for a number of reasons. In addition to the presence of the deep marsupium, the tent of mucus that the peripetalous fasciole would have throw over the marsupium would also have protected the young echinoids. Furthermore, the larger spines that arched over the petals from interambulacra 2 and 3 would have provided a protective advantage. Orientation of the prominently crenulate tubercles provides evidence that the spines would not have extended perpendicular to the test, but at a very low angle, almost tangential, to the surface of the test across the petals. Finally, the young echinoids would also have been protected from predators by the sediment that would have covered the entire aboral surface of the test.

The absence of pore pairs in the vicinity of the apical system in *Hysteraster paragrapsimus* and reduction in size of the pore pairs in the anterior row of the anterior petals, combined with the absence of pore pairs in the marsupium in the two species of *Peraspatangus*, suggest that their reduction may be related to the presence of brooded juveniles in the marsupium. Brooding in ambulacral marsupia can only be effective if tube feet are reduced in size to allow sufficient space in the petals to accomodate the juveniles. If this is the case then it is likely that the brooded juveniles were concentrated in the area immediately surrounding the apical system, along the anterior part of the anterior petals, and perhaps in the central part of the posterior petals, between the pore pairs. It is worth considering whether the presence of reduced pore pairs in the anterior row of the anterior paired petals in other spatangoids, such as *Atelospatangus, Paramaretia, Nacospatangus* and *Agassizia,* is indicative of these echinoids also being brooders.

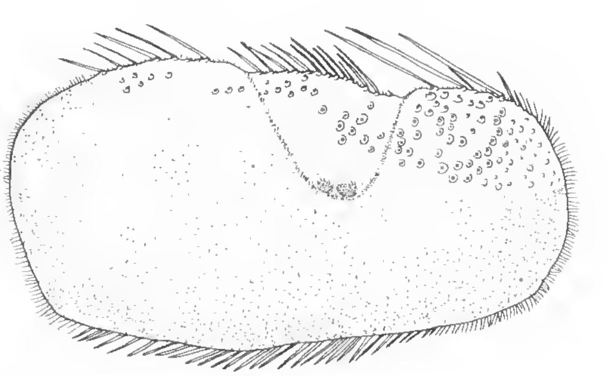

FIGURE 5. Restored profile of *Hysteraster paragrapsimus* gen. et sp. nov. ♀, showing course of peripetalous fasciole, distribution of primary tubercles and extent of maximum known development of marsupium. Spine orientation based on data from tubercles; spine length conjectural.

ACKNOWLEDGMENTS

We would like to thank Neville Pledge of the South Australian Museum for the loan of specimens, Frank Holmes for his help with information and Kris Brimmell for photography.

REFERENCES

DAVID, B., LAURIN, B. & DE RIDDER, C. 1988. How *Echinocardium cordatum* (Pennant) shows sexual dimorphism. Pp. 683-686 *in* 'Echinoderm Biology'. Eds R. D. Burke, P. V. Mladenov, P. Lambert & R. L. Parsley. Balkema Rotterdam.

EMLET, R. B. 1989. Apical skeletons of sea urchins (Echinodermata: Echinoidea): two methods for inferring mode of larval development. *Paleobiology* **15**: 223–254.

JAGT, J. W. M. & MICHELS, G. P. H. 1990. Additional notes on the echinoid genus *Cyclaster* from the Late Maastrichtian of northeastern Belgium. *Geologie en Mijnbouw* **69**: 179–185.

KIER, P. M. 1967. Sexual dimorphism in an Eocene echinoid. *Journal of Paleontology* **41**: 988–993.

KIER, P. M. 1969. Sexual dimorphism in fossil echinoids. Pp. 215-222 *in* 'Sexual Dimorphism in Fossil Metazoa and Taxonomic Implications'. Ed. G. E. G. Westermann. E. Schweizerbart'sche Verlagsbuchhandlung: Stuttgart.

KRUSE, P. D. & PHILIP, G. M. 1985. Tertiary species of the echinoid genus *Eupatagus* from southern Australia. *Special Publication, South Australian Department of Mines and Energy* **5**: 167–185.

LAMBERT, J. 1933. Échinides de Madagascar communiqués par M. H. Besairie. *Annales Géologiques du Service des Mines, Madagascar* **3**: 1–49.

LINDSAY, J. M. 1985. Aspects of South Australian Tertiary foraminiferal biostratigraphy, with emphasis on studies of *Massilina* and *Subbotina*. *Special Publication, South Australian Department of Mines and Energy* **5**: 187–231.

LUDBROOK, N. H. 1961. Stratigraphy of the Murray Basin in South Australia. *Bulletin of the Geological Survey of South Australia* **36**: 1–96.

LUDBROOK, N. H. 1969. Tertiary Period. Pp. 172-203 *in* 'Handbook of South Australian Geology'. Ed. L. W. Parkin. Geological Survey of South Australia, Adelaide.

MCKINNEY, M. L. 1988. Roles of allometry and ecology in echinoid evolution. Pp. 165-173 *in* 'Echinoderm Phylogeny and Evolutionary Biology'. Eds C. R. C. Paul & A. B. Smith. Clarendon: Oxford.

MCNAMARA, K. J. 1985. Taxonomy and evolution of the Cainozoic spatangoid echinoid *Protenaster*. *Palaeontology* **28**: 311–330.

MCNAMARA, K. J. 1991. A guide to the echinoids of the Middle Miocene Rutledge Marl, Victoria. *Victorian Naturalist* **108**: 8–19.

MCNAMARA, K. J. & PHILIP, G. M. 1980. Australian Tertiary schizasterid echinoids. *Alcheringa* **4**: 47–65.

MCNAMARA, K. J. & PHILIP, G. M. 1984. A revision of the spatangoid echinoid *Pericosmus* from the Tertiary of Australia. *Records of the Western Australian Museum* **11**: 319–356.

MCNAMARA, K. J., PHILIP, G. M & KRUSE, P. D. 1986. Tertiary brissid echinoids from southern Australia. *Alcheringa* **10**: 55–84.

PHILIP, G. M. 1963. The Tertiary echinoids of south-eastern Australia. I. Introduction and Cidaridae (1). *Proceedings of the Royal Society of Victoria* **76**: 181–236.

PHILIP, G. M. 1964. The Tertiary echinoids of south-eastern Australia. II. Cidaridae (2). *Proceedings of the Royal Society of Victoria* 77: 433–477.

PHILIP, G. M. 1965. The Tertiary echinoids of south-eastern Australia. III Stirodonta, Aulodonta, and Camarodonta (1). *Proceedings of the Royal Society of Victoria* 78: 181–196.

PHILIP, G. M. 1969. The Tertiary echinoids of south-eastern Australia. IV. Camarodonta (2). *Proceedings of the Royal Society of Victoria* 82: 233–275.

PHILIP, G. M. & FOSTER, R. J. 1971. Marsupiate Tertiary echinoids from south-eastern Australia and their zoogeographic significance. *Palaeontology* **14**: 666–695.

ROMAN, J. 1983. Échinides 'marsupiaux' (Fam. Temnopleuridae) dans le Néogène de l'Ouest Européen. *Annales de Paléontologie* **69**: 13–42.

SMITH, A. B. 1984. 'Echinoid Palaeobiology'. George Allen and Unwin: London.

WRAY, G. A. & RAFF, R. A. 1991. The evolution of developmental strategy in marine invertebrates. *Trends in Ecology and Evolution* **6**: 45–50.